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Epiphyll specialization for leaf and forest successional stages in a tropical lowland rainforest

Short running title: Epiphyll specialization for succession

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Abstract

Questions

The importance of tropical rainforest gap dynamics in biodiversity maintenance is not fully understood, in particular for taxa other than trees and lianas. We used epiphylls on rainforest leaves to study the importance of leaf- and forest-scale succession in determining biodiversity patterns by characterizing community change with leaf age in gaps and closed-forest habitats. We asked: 1. Do epiphylls show specialization for leaf and forest successional stages? 2. Can early and late-successional epiphyllous species be recognized at these two scales? 3. How do epiphyll presence, species richness, and cover change with leaf and forest successional stages?

Location

Barro Colorado Island, Panama.

Methods

Data were collected from 420 leaves, in three age groups and at two heights on shrubs in gaps and closed forest. We calculated turnover and nestedness components of dissimilarity to evaluate the importance of species replacement or accumulation during leaf and forest succession. Using generalized linear mixed models we determined what factors explain epiphyll species occurrence, richness and cover.

Results

Closed forest contained more liverwort and lichen specialist species than gaps. Specialist species were identified for older leaves only. Dissimilarity between leaves within age groups was dominated by turnover within and between forest successional stages. Dissimilarity between leaf age groups, at the site level, was dominated by nestedness, i.e. species accumulation. Both in forest and gaps, epiphyll presence and cover increased with leaf age for all taxa except fungi, while species richness increased only for lichens.

Conclusion

Early and late forest successional stages both contribute to epiphyll species richness by harboring specialized species. Among leaf successional stages, young leaves contain a mere subset of the species found on older leaves. Epiphyll communities do not follow classic succession, in the sense of changes being driven by species replacement, but are characterized by species accumulation through time.

Keywords

Bryophytes, lichens, fungi, epiphylls, specialists, forest gaps, community dynamics, succession, species accumulation.

INTRODUCTION

Forest gap dynamics enhance habitat heterogeneity in tropical forests and play an important role in maintaining the high diversity of woody species such as trees and lianas in these forests (Schnitzer & Carson, 2001; Sharma, Grytnes, Måren, & Vetaas, 2016; Terborgh, Huanca Nuñez, Alvarez Loayza, & Cornejo Valverde, 2017, Villa et al., 2018). Even though the species richness of woody species in gaps may not be greater than in the adjacent closed forest (Sharma et al., 2016), the conditions typical of gaps, in particular the high light levels, allow a specialized set of species, including many lianas (Malizia & Ricardo, 2008), to establish and quickly colonize these spaces. Such species may dominate locally until more competitive tree species take over (Poorter et al., 2019). As new gaps are formed continuously, the early-successional species are able to maintain viable populations within the forest ecosystem. Although intuitive, the long hypothesized importance of gap dynamics, or more generally, of habitat heterogeneity, for maintaining tropical forest biodiversity (Ricklefs, 1977; Denslow, 1980) is still not fully understood (Baker et al., 2016; Sharma et al., 2016). For instance, treefall disturbances did not increase beta-diversity of woody species composition in disturbed versus undisturbed forest patches, even if species richness was higher in disturbed sites in Peru, Brazil and French Guiana (Baker et al., 2016).

Most studies assessing the role of treefall disturbance in maintaining species diversity focus on soil-rooted woody plants, while other components of the forest, in particular, structurally-dependent plants such as epiphytes (growing on stems and branches) and epiphylls (growing on leaves), are less studied (Lücking, 1999a; 1999b; Marino & Salazar Allen, 1992).

Bryophytes and lichens, including many specialized epiphylls, represent a significant proportion of diversity in tropical forests (Gradstein, 1992; Pócs, 1982). These organisms are often overlooked, because of their relatively small size and challenging identification. Epiphyllous lichens have been classified according to their preference for open or closed habitats (Lücking, 1997; Lücking, 1999b), and there is some indication that gaps are probably important in maintaining epiphyll diversity (Lücking, 1999b). Epiphyllous lichen diversity is greater in the transition between closed forests and gaps (Lücking, 1997). However, the degree of specialization of different epiphyll species and the variation of this specialization within and among taxonomic groups (e.g. lichens and liverworts) is unknown.

Unlike for woody plants, there is no succession of epiphylls from gap creation to gap closure, simply because the substrate of these organisms, i.e., leaves, are generally replaced several times within the life span of a forest gap. In tropical forests, leaves of trees and shrubs may persist for up to 12 years in the shade, with a mean leaf life span of about 11 months in gaps and 22 months in the shade (Kitajima, Cordero, & Wright, 2013). Gaps can exist much longer than that and may take about 35 years to develop a mature canopy structure (Martinez-Ramos, Alvarez-Buylla, Sarukhan, & Pinero, 1988). Leaf age has been identified as an important factor determining epiphyll cover (Coley, Kursar, & Machado, 1993; Roberts, Nelson, Adams, & Palmer, 1998) and succession of epiphyll communities takes place with leaf aging both in gaps and in the forest understorey (Olarinmoye, 1975; Conran, 1997; Conran & Rogers, 1983; Rogers, 1995). Additionally, the course of this epiphyll succession in forest gaps may be modified by changes in environmental conditions, e.g. light (Marino & Salazar Allen, 1992; Lücking, 1999b) and humidity (Lücking, 1998a; 1998b; Sonnleitner, Dullinger, Wanek, & Zechmeister, 2009), during gap succession. Treefall gaps and closed forest provide different habitats that may show different successional patterns of their epiphyll communities. Nonetheless, the succession of epiphylls on aging leaves has never been studied in relation to gap dynamics.

Generally, epiphyll succession begins with fungi and algae, while lichens and bryophytes come in later (Lücking & Bernecker-Lücking, 2002; Ruinen, 1961). How the species from each group interact with each other to determine the course of succession is unknown. It has been suggested that epiphyllous liverworts can outcompete lichens, but never the other way around (Coley et al., 1993). There have been some attempts to classify epiphyll species into early and late-successional species. For lichens, pioneer species were observed to be replaced by a competitive and widespread species on leaves of the Australian rainforest tree *Wilkiea macrophylla* (Conran & Rogers, 1983), while for epiphyllous liverworts late-successional species and generalist species have been distinguished on leaves of various tree species in Nigeria (Olarinmoye, 1975). Although these studies indicate that epiphylls indeed show specialization for early and late-successional stages on leaves, the generality of these findings still awaits to be demonstrated.

The aim of the present study is to understand how epiphyll community composition and species richness change with a leaf age and how these changes differ between gaps and closed-

forest habitats. The importance of the successional stage is thus addressed at two spatial scales: at the leaf scale, among leaves of different ages, and at the forest scale (gaps and closed-forest habitats representing early and late-successional stages in forest development, respectively). We address the following research questions: 1. Do epiphyll taxa show specialization for leaf ages and microsites (closed forest and gaps) and how is specialization distributed among lichens and liverworts? 2. Can early and late-successional epiphyllous species be recognized and are these the same in different microsites? And 3. How do epiphyll presence, species richness and cover change with leaf age and how do these changes depend on microsites, leaf age, vertical leaf location and leaf texture within these sites?

We hypothesized that 1) epiphyllous lichens are more often gap specialists and liverworts are more often closed-forest specialists (Lücking, 1997), 2) only a subset of species is able to colonize young leaves, i.e., it is possible to distinguish pioneer and late-successional species, 3) epiphyllous lichens have a greater proportion of species that are pioneers than do liverworts, 4) early-successional epiphyllous species behave more like generalists (opportunistic) than late-successional species do, so that early-successional epiphyll communities (on young leaves) are more similar among microsites than late-successional communities, and 5) epiphyll presence, richness and cover increase with leaf age in both gaps and closed-forest sites (Roskoski, 1981).

MATERIALS AND METHODS

Study site

The study was conducted in the tropical lowland forest on Barro Colorado Island (BCI, N09^{o}09’24.6’’, W79^{o}50’42.1’’), located in the lake that formed after construction of the Panama Canal, in Panama. The dry season generally lasts from mid-December until the end of April, with on average as little as 285 mm of rain during this whole period, and the wet season lasts from May until mid-December. Mean annual rainfall is 2623 mm and temperature varies little throughout the year (Paton, 2018), with an average daytime temperature of 32°C and an average night-time temperature of 23°C.

Study design and sampling

Leaves were selected in two types of microsite, representing forest successional stages: closed forest and forest gaps. Here we define a forest gap as a visible opening in the forest canopy after a natural disturbance, i.e. a treefall. Gap size varied between ~ 400 m^2 and ~2500 m^2.

Fourteen sites, with seven each in both microsite types, were selected across BCI (Appendix S1). At each site, five healthy tree saplings or shrubs with a minimum height of 1.2 m were selected within a 20x20 m plot. These hosts belonged to 26 species. On each, leaves were sampled in two height groups (<0.9 m and between 1.0 and 2.0 m) and three age groups (young, medium-aged and old leaves, Fig. 1). This resulted in six leaves per host and 420 leaves in total per site. The leaf age groups were based on the leaf location on the host branch, with the youngest leaves growing closer to the branch tip. They represent a chronosequence per host but are not defined by absolute ages.

The epiphyll cover was assessed with photographs taken with a digital camera (Canon EOS Rebel T1i). All photographs were taken from a similar angle and distance while leaves were kept as flat as possible. Leaf texture (matt vs. shiny) was evaluated through visual observation. Species richness and cover per epiphyll taxon (only for lichens and liverworts) were estimated based on manually digitized epiphyll patches using ArcMap 10.5. Lichens and liverworts were identified to species and morphospecies (different taxonomic levels: genus and family) whenever possible. Unidentified lichen or liverwort patches (126 in total) were not considered in most data analyses (see the data analysis subsections below). Algae and fungi were not differentiated into species or morphospecies. Species nomenclature follows Lücking (2008) for lichens and Söderström et al. (2016) for liverworts. The lichen and liverwort vouchers are deposited at the University of Panama herbarium (PMA).

Relative humidity (RH) and temperature (T) were registered every 30 minutes from the 1st to 31st of December 2016 (wet season) and from the 1st to the 28th of February 2017 (dry season) using dataloggers (Humilog "rugged", Driesen & Kern and Hobo Pro v2, Onset), which were placed at 1.5-m height in the center of each site (seven days in each of the 14 sites during each season). Due to the limited number of dataloggers, we could not measure all sites simultaneously. Additionally, for each leaf, canopy openness was determined from hemispherical photographs taken using a small fish-eye lens on a Samsung J1 cell phone camera according to Tichý (2016) and using the Gap Light Analysis Mobile Application, version 3 (Lubomír Tichý, 2015).

Data analysis

Microclimatic differences

Differences in microclimate between the seven closed-forest and seven gap sites were assessed by means of an ANOVA. Microclimatic variables included average of mean, maximum and minimum daily T and the average of mean and minimum daily RH for the wet and dry season, i.e. with one value per variable per site. To assess differences in canopy openness (response variable) above each leaf among microsites (predictor variable), we used a generalized linear mixed model (GLMM, negative binomial family) with site as a random effect using the 'glmmTMB' package (Brooks et al., 2017).

Specialist species

To detect epiphyllous species that may be indicative or specialized for 1) particular leaf ages along the chronosequences, 2) microsite, 3) vertical leaf location or 4) leaf texture, indicator species analyses were carried out using species cover data. We applied the analyses to a subset of the data excluding singletons and doubletons, as well as unidentified lichen and liverwort patches. The indicator value can vary from 0 (random distribution) to 1 (species present on all leaves within a group and not present in other groups). The indicator value thus shows the association between a species and a group (Dufrêne & Legendre, 1997; De Cáceres, Legendre, & Moretti, 2010). Statistical significance of the indicator value was calculated using permutation tests (999 permutations). The indicator species analysis was carried out with the package 'indicspecies' (De Cáceres & Legendre, 2009).

Dissimilarity in species composition

We assessed the dissimilarity of epiphyll communities and to what extent compositional changes on leaves involves species replacement or accumulation and whether these processes differ between microsites. To this end, we calculated the turnover or Simpson dissimilarity (β_{sim}) and nestedness (β_{sne}, the nestedness component of Sørensen dissimilarity); both components of Sørensen dissimilarity (total Sørensen; Baselga & Orme, 2012). Turnover indicates species replacement (spatially or temporally); whereas nestedness indicates species loss (or gain) or that the poorest assemblage is a strict subset of the richest one (Baselga & Orme, 2012).

We used species presence/absence data and analyzed only the lichen and liverwort datasets, including morphospecies but not the unidentified patches.

Dissimilarity components were calculated between even-aged leaves within and among microsite types using the beta.multi function from the 'betapart' package (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2018). This analysis was repeated at the site scale, to assess how much the scale affected the outcome and hence the validity of assessing temporal changes (see below) at the microsite scale.

We assessed directional changes (temporal changes) from young to older leaves using the chronosequence as a proxy for points in time, using the beta.temp function of the same package. In this case, the analysis was done at the site level, treating the grouped young, middle-aged and older leaves, respectively, within a site as though they were repeated measurements through time. We compared total nestedness, turnover, and dissimilarity on leaves between closed-forest sites and gaps using a Mann-Whitney test.

Explaining variability in community structure

To understand the gradients shaping epiphyll community structure, a canonical correspondence analysis (CCA) was carried out using microsite, leaf texture, vertical leaf location, leaf age as constraining variables. We used the same data as in the indicator species analyses. The best model was found by stepwise backward selection and the significance of variables was assessed by an ANOVA like permutation test (999 permutations). Variance inflation factor was used to check independence of variables. CCA was conducted using the 'vegan' package (Oksanen et al., 2018).

Explaining the variability of species presence, richness, and cover

To understand which ecological variables (microsite, leaf texture, vertical leaf location within host, and leaf age) determine species presence (modelled as probability of occurrence), richness, and a cover of each epiphyll taxa we used GLMMs (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The occurrence probability was modelled separately from species richness and cover because our data were strongly zero-inflated, with most zeros being concentrated on the young leaves. This approach yields the same results but has more flexibility in its implementation than formal hurdle models (Brooks et al., 2017). For the probability of occurrence, all data were used, while for species richness

and cover, only leaves with positive values were included in the analysis. We thus included morphospecies at all levels (genus, family) and unidentified liverwort and lichen patches (with an average 0.31±0.47 patches per leaf).

For occurrence probability we used a Binomial distribution and for the species richness and cover data we used the truncated negative binomial distribution with a Log Link function. Site was included as a random effect. Tested response variables also included the interactions age:microsite, age:vertical leaf location, microsite:vertical leaf location. The best models were selected using backward stepwise selection based on Likelihood Ratio Tests. Significance of each variable was calculated with the Anova function using the 'car' package and differences between factor levels were assessed using Tukey-adjusted comparisons from the 'emmeans' package (Lenth, 2018).
All analyses were carried out with the R software version 3.5.1 (R Core Team, 2018).

RESULTS

In total, we identified 54 lichen species and 10 liverwort species (Appendix S2), plus 13 morphospecies (eight lichens and five liverworts). Only two of the 420 leaves were empty, while 103 leaves had unidentifiable patches together with other epiphylls and seven leaves had only unidentifiable patches. The most common epiphyllous species was the liverwort *Leptolejeunea elliptica* (Appendix S2) which occurred on 34% of all leaves and had a high total cover.

Three out of the five most abundant species on young leaves (*L. elliptica, Porina karnatakensis*, and *Coenogonium* sp.) were also among the most abundant species on older leaves, increasing strongly in total cover with leaf age, indicating the persistence of dominance (Fig. 2). Differences in microclimatic variables between microsites were observed only for the wet season, where mean daily maximum temperature was significantly higher in gap than in forest sites (by 1.8°C), whereas mean daily minimum and average air humidity were significantly higher in the closed-forest than in gap sites (by 8% and 2%, respectively). Canopy openness was significantly higher in gap than in forest sites, but with 4% and 5% it was very low in both sites (Appendix S3). This low openness is partly because the measurement was taken at the leaf level, so that close-by leaves could cover large portions of the sky view. Overall, although not quantified by our data, the gaps were clearly lighter than the closed forest.

Epiphyll specialization

Here we define a 'specialist' as a species showing a significant indicator value, irrespective of the strength of the value. Low indicator values imply that the species may be also found in other categories. Overall, no specialists were found for young leaves and medium-aged leaves (Appendix S2). Indicator species analysis divided specialists along the chronosequence into two groups: old-leaf specialists alone (nine lichen species with indicator values between 0.24 and 0.55) and medium-aged-leaf and old-leaf specialists combined (one lichen species with an indicator value of 0.43). Only lichens but not liverworts showed specialization for leaf ages.

In total 18% of all lichen and liverwort taxa (excluding singletons and doubletons) were specialists for either microsite type (Appendix S2). Both liverwort and lichen specialists were more common, almost two-fold, in closed-forest sites (0.19 - 0.49) than in gap sites (0.23 - 0.75). Only four specialists were found for the vertical leaf location with indicator values between 0.18 and 0.27. One lichen species was a lower leaf location specialist (and also a closed-forest specialist) and two liverwort and one lichen species were higher vertical leaf location specialists. More specialists were found for matt leaves (seven lichen species, 0.20 - 0.53) than for shiny leaves (one lichen and one bryophyte species, 0.27 - 0.35).

Dissimilarity in species composition

Generally, compositional dissimilarity among leaves of the same age was very high (over 80%). Within and among microsites, and whether analysed at the leaf or site scale, dissimilarity within leaf age classes was mostly driven by turnover, while nestedness contributed very little (Appendix S4 & S5).

Changes along the chronosequences, as a proxy for "temporal" changes, indicated that, in contrast to the dissimilarity between microsites (Fig. 3), the temporal changes in epiphyll composition were largely driven by nestedness, both in the closed forest and in gaps. This indicates that dynamics are driven by species accumulation rather than replacement.

Explaining variability in community structure

Epiphyllous lichen and liverwort community structure was extremely variable, but still some of it could be explained by leaf age, microsite and vertical leaf location (Appendix S6). The first CCA axis explained only 1.3% of the variation and was correlated with the microsite (gaps and closed forest) and leaf age. The second CCA axis explained even less: 0.01% and was correlated with leaf age (young vs. middle-aged and old leaves) and vertical leaf location. Liverwort and lichen taxa did not separate out strongly in their distribution along the gradients, although there is a tendency for liverworts to be located closer to the lower leaf location / closed forest and for lichens to be towards the higher leaf location / gap end of the axes (Appendix S6).

Epiphyll presence, richness, and cover in association with environmental variables

Epiphyll presence, modelled as the occurrence probability, was driven by leaf age for most of the taxa (Table 1, Appendix S7 a,b,c,d,e, S8). Occurrence probability was highest on older leaves for most of the taxa, except for fungi (Appendix S7 a,c,e, S9). In contrast to all other taxa, fungi occurred less on old leaves than on young and medium-aged leaves. Liverwort occurrence probability was significantly higher on young leaves in gaps than on young leaves in closed-forest sites. Liverwort occurrence probability became comparable on older leaves of both gaps and closed-forest sites (Appendix S7 e) and it was significantly higher on lower leaf locations in gaps than at the same location in closed-forest sites.

Total epiphyll and lichen occurrence probabilities were higher on matt leaves than on shiny ones (Appendix S7 b,d), while the opposite trend was observed for algae (Appendix S8).

Total and lichen species richness were significantly higher on old leaves than on young or medium-aged leaves (Fig. 4a, b, Table 1). Liverwort species richness variability could not be explained by any of the variables (Table 1).

All taxa increased in cover with leaf age (Table 1, Appendix S8, S9, S10, S11, S12, S13, S14). The total cover was greater on the lower leaves in gaps, but no difference between vertical leaf locations was found in the closed-forest sites (Appendix 10 b). Lichen cover was higher in lower than in higher leaf locations for medium-aged leaves, but not for young or old leaves (Appendix 10 e). Liverwort cover was higher in gaps independently of leaf location, whereas in closed-forest sites it was higher on lower than on higher leaf locations (Appendix 10 g).

DISCUSSION

Epiphyll community composition in the rainforest of Barro Colorado Island varied along forest-level as well as leaf-level successional stages. Both closed forest and gaps were important in contributing to epiphyll diversity, each microsite harboring specialized species, although these were not exclusive. At the forest level, dissimilarity of evenly-aged leaves was very high both within and between microsite types and was dominated by turnover, indicating a low overlap of species among leaves. In contrast, changes in epiphyll communities between leaf age groups were dominated by nestedness, suggesting that epiphyll dynamics are driven by an accumulation, rather than a replacement, of species during leaf aging. Accordingly, three of the five species that were most abundant on young leaves also dominated on older leaves, the other two persisting without increasing in cover.

Epiphyll specialization for forest successional stages

In contrast to our hypothesis that epiphyllous lichens would be found more often as gap specialists and liverworts as closed-forest specialists, both lichens and liverworts had more specialists in closed-forest sites than in gaps, although no species was exclusive to either microsite type. This contrasts with the results of Lücking (1999b), who reported twice as many lichen species associated with gaps than with shady understories. Our findings also do not confirm the well-known statement that lichens prefer lighter and tolerate drier conditions and liverworts need humid conditions (Dyer & Letourneau, 2007; Gradstein, 1992; Lücking, 1997). No strong separation of these main taxonomic groups was found along the first two axis of the CCA, indicating that they are similarly distributed in ecological space. While microsite significantly explained the variability of epiphyll community structure, the very low explanatory power of the CCA axes indicates that there is no clear distinction of closed-forest and gap communities. This contradiction might be related to the relatively dry climate in our study site (Condit, Pérez, Lao, Aguilar, & Hubbell, 2017), favoring lichens relative to liverworts even inside the forest. Also, our forest has a higher level of deciduousness than other tropical forests, even those nearby on the banks of the Panama Canal (e.g. 3 % of leaf density during the dry season at Shermann and 10 % on BCI after Condit et al., 2004), allowing more light to reach the forest understorey and reducing the difference with forest gaps, at least during part of the year.

We found no effect of microsite type on liverwort species richness, which is in line with those findings of Olarinmoye (1975), who found a similar number of epiphyllous liverwort species in open and shaded sites in lowland semi-deciduous forest plantations and closed-forest sites in Nigeria. These sites have a mean annual rainfall of 1143-2072 mm (Hopkins, 1966, Sanford, 1969), slightly less than our study site.

The low explanatory power of the CCA indicates that leaves are highly unique in their species composition, while also additional factors might better explain epiphyll community variation, e.g. spatial structure or host species. Epiphyll communities have been shown to differ among host species (Conran, 1997; Lücking, 1998a; 1998b), which probably may also explain part of the unexplained variation in our study. Due to the high diversity and low replication of host species, we could not test this, but the importance of host identity relative to other drivers of diversity would be a worthwhile question for future studies.

Epiphyll specialization for leaf successional stages

It was possible to distinguish specialized late-successional lichen species, i.e. species that mostly occurred on old or medium-aged and old leaves, but no early-successional specialists. Even the late-successional specialists were not found exclusively on older leaves, but they were particularly abundant there, relative to the youngest leaves. It is possible that some or all of these `specialized late-successional species´ were already present on young leaves, but we were not able to identify them, given the immature nature of the patches. However, there are also possible mechanisms that would preclude some species from colonizing young leaves. For example, leaf surfaces change with age (an increase of dust, debris, damage) providing specific microhabitats (Monge-Nájera & Blanco, 1995) probably more suitable for the germination of particular fungi spores or for fungi hyphae to surround the algae and develop a lichen (Sanders & Lücking, 2002).

No early-successional specialists could be identified among the epiphyllous lichens and liverworts, i.e. none occurred preferentially on young leaves or medium-aged leaves. This does not contradict our hypothesis that only a subset of species is able to colonize young leaves. Instead, it shows that the pioneer species colonizing young leaves are not replaced by late-successional species. Species are establishing continuously throughout leaf development while young leaf colonizers also

persist on the leaves. This is also shown by the very low turnover and high nestedness driving temporal changes in species composition between leaf ages. It agrees with a study on epiphyllous liverworts in a humid premontane tropical rainforest in Panama, which concluded that most early colonizers persist throughout the entire leaf age sequence (Sierra, Toledo, Salazar Allen, & Zartman, 2018). Pioneer species possibly facilitate the subsequent colonization by late-successional species but are not replaced by them. As a result, epiphyll cover and species richness increase strongly with leaf age, with the exception of fungi.

The hypothesis that epiphyllous lichens would be more often found as pioneers in comparison to liverworts was not supported but could also not be refuted. Lichen species richness on young leaves may have been largely underestimated, as many small lichen patches (~0.5-2 mm) could not be identified, thus potential pioneer species went unrecognized.

The first colonizers in most cases were fungi (non-lichenized or non-lichenicolous), which appeared as black dots on the leaf surface. Ruinen (1961), in a study in Indonesia, found that fungi are among the first colonizers on young leaves after bacteria and that succession continues with algae, lichens, and bryophytes. Richards (1952) found that lichens and algae are the earliest colonizers on leaves in tropical rainforests and in favorable conditions succession continues with liverworts eliminating lichens and algae. In contrast, such a clear replacement process we did not observe. Olarinmoye (1975), in Western Nigeria, suggested that the first most abundant species established on a leaf will be dominant (priority effect; e.g. Chase, 2003; Fukami, 2015) in later stages of epiphyllous liverwort succession. In accordance, we found that three of the five most common species on young leaves also dominated on older leaves, thus retaining their dominance along the chronosequence (Fig. 2). However, the strength of the priority effect should ideally be tested by following communities on single leaves through time or by controlled experiments (e.g. Collinge & Ray, 2009; Dickie, Fukami, Wilkie, Allen, & Buchanan, 2012).

The hypothesis that early-successional epiphylls behave more like generalists (opportunistic) than late-successional species could not be confirmed: epiphyll communities on young leaves were not more similar among microsites than late-successional communities.

Differences in epiphyll community changes among forest successional stages

The hypothesis that epiphyll presence, species richness, and cover increase with leaf age in both gaps and closed-forest sites was mostly supported, although liverwort species richness did not differ according to leaf age or microsite.

The increase in cover and richness with leaf age was due to an accumulation, rather than a replacement of species. Our study suggests that classical succession (Connell & Slatyer, 1977) does not take place in this epiphyllous community, since species accumulation, instead of species replacement, is the main mechanism behind the dynamics. A similar mechanism was also found driving epiphyllous lichen dynamics in a subtropical rainforest in Australia (Rogers, 1995), based on a chronosequence, where only one lichen species out of seven disappeared towards later successional stages. Further chronosequence studies indicate that the same mechanism may drive the dynamics of cryptogams at different scales in forest ecosystems: along an age gradient of oak branches for epiphytic lichens (Stone, 1989), during secondary forest succession in a Tasmanian wet eucalypt forest for epixylic bryophytes (Browning et al., 2010), and along the ontogeny of beech trees for epiphytic bryophytes and lichens (Kaufmann, Hauck, & Leuschner, 2018). Evidence of the contrary, replacement as the main driver of cryptogam dynamics, has also been found in some studies. For instance, terricolous bryophyte communities changed from feathermosses to *Sphagnum* species forming hummocks and then to *Sphagnum* species forming hollows in forest stands after a fire (Fenton, Bergeron, & Nicole, 2006). In the dynamics of saxicolous and terricolous bryophyte and lichen communities in an Antarctic glacial valley, turnover dominated, although some pioneer species remained throughout the succession (Favero-Longo et al., 2012). Other studies provide mixed signals. For example, both species replacement and accumulation were found to drive secondary succession in different-aged deciduous and coniferous forests after a fire in boreal Alaska (Jean, Alexander, Mack, & Johnstone, 2017) and for epiphytic lichens on aspen trees of different age in Great Britain (Ellis & Coppins, 2006) and in the southern Rocky Mountains, USA (Rogers & Ryel, 2008). Evidence thus suggests that the dynamics of bryophyte and lichen communities often have a strong component of nestedness, i.e. species accumulation through time, relative to species replacement through competition. A reason may be the focus on stress tolerance rather than competitive abilities in many of these species. Although, like many of the other examples presented, our results are based on

chronosequences, we assume that epiphyll species accumulation would be also observed when following individual leaves through time.

CONCLUSIONS

Our results show that even at the relatively small scale of single leaves, epiphyllous communities are rich and are shaped by the heterogeneous environment at both the leaf and forest scale. Although closed-forest sites contained more specialized species, gaps also harboured some almost exclusive species and thus appear to contribute to epiphyll diversity maintenance as they do for vascular plants (Dechnik-Vázquez, Meave, Pérez-García, Gallardo-Cruz, & Romero-Romero, 2016; Terborgh et al., 2017). It should be kept in mind though that for epiphylls, unlike for ground-rooted plants, the presence of these ´gap´ species in higher strata in the closed forest cannot be excluded. Our results suggest that epiphyll communities in the studied tropical lowland forest do not follow a classical succession pattern but instead show species accumulation throughout leaf aging. An interesting next step would be investigating the interactions between early colonizers and later arrivals, through spatial analyses of species locations, and through analyzing changes on single leaves followed through time.

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AUTHOR CONTRIBUTIONS

AM, NSA, MYB designed the study. AM did the field work. AM and NSA identified the species. AM and GML performed statistical analysis. AM, MYB and GML wrote the manuscript with inputs from NSA.

DATA ACCESSIBILITY

Data are available in Dryad Digital Repository: https://doi.org/10.5061/dryad.q83bk3jdh.

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Table 1. The output of GLMMs for epiphyll occurrence probability, richness and cover per taxonomical group. VLL refers to vertical leaf location. Data from epiphylls in closed forest and gaps on Barro Colorado Island, Panama. Final models were obtained with stepwise backward selection and include site as random effect (not shown). For liverwort species richness no significant predictors were found, for algae and fungi species were not identified so that richness is not analyzed.

Response	Predictors	Occurrence probability		Richness		Cover	
		Chisquare	*p*	Chisquare	*p*	Chisquare	*p*
Total							
	Leaf age	44.43	<0.01	130.67	<0.01	547.28	<0.01
	Leaf texture	4.64	<0.05			14.69	<0.01
	VLL					13.94	<0.01
	Microsite					0.01	0.91
	Microsite:VLL					8.67	<0.01
Lichens	Leaf age	53.42	<0.01	84.65	<0.01	240.58	<0.01
	Leaf texture	5.29	<0.05			36.36	<0.01
	Microsite					11.60	<0.01
	VLL					5.19	<0.05
	Leaf age:Microsite					14.41	<0.01
	Leaf age:VLL					9.58	<0.01
	Microsite:VLL					9.35	<0.01
Liverworts							
	Leaf age	32.00	<0.01			36.81	<0.01
	Microsite	2.96	0.09			5.76	<0.05
	VLL	1.13	0.29			11.30	<0.01
	Leaf age:Microsite	10.14	<0.01				
	Microsite:VLL	9.10	<0.01			5.35	<0.05
Algae							
	Leaf age	40.50	<0.01			34.04	<0.01
	Leaf texture	7.07	<0.01				
	Microsite	4.38	<0.05				
	VLL					4.19	<0.05
Fungi							
	Leaf age	24.27	<0.01			6.29	<0.05
	Microsite					<0.01	0.99
	Leaf age:Microsite					9.36	<0.01

Figure 1. Example of leaves showing an accumulation of epiphylls along a chronosequence in the rain forest of Barro Colorado Island (Panama). Young, medium-aged, and old leaves (from left to right) of the host species *Mourini myrtilloides* in the Shannon gap site. Epiphylls show as light green threads (liverworts), pale brownish (algae), dark brownish (fungi) and blue-grey (lichen) patches on the older leaves. The black and white scale bars correspond to 1 cm.

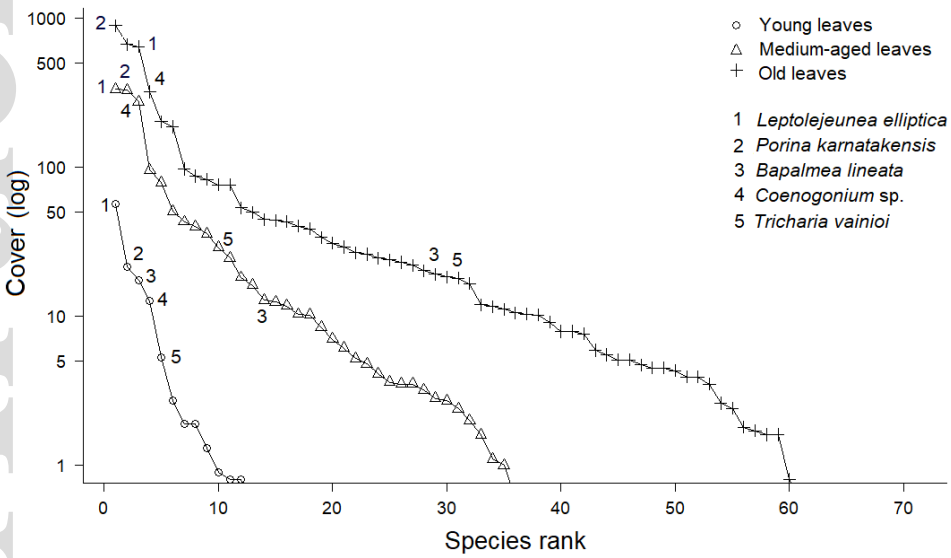

Figure 2. Rank-abundance curves for each leaf age group, ranked according to total cover on leaves in the rain forest of Barro Colorado Island (Panama). Data include morphospecies but exclude unidentified patches. Curves were calculated using the BiodiversityR package (Kindt & Coe, 2005).

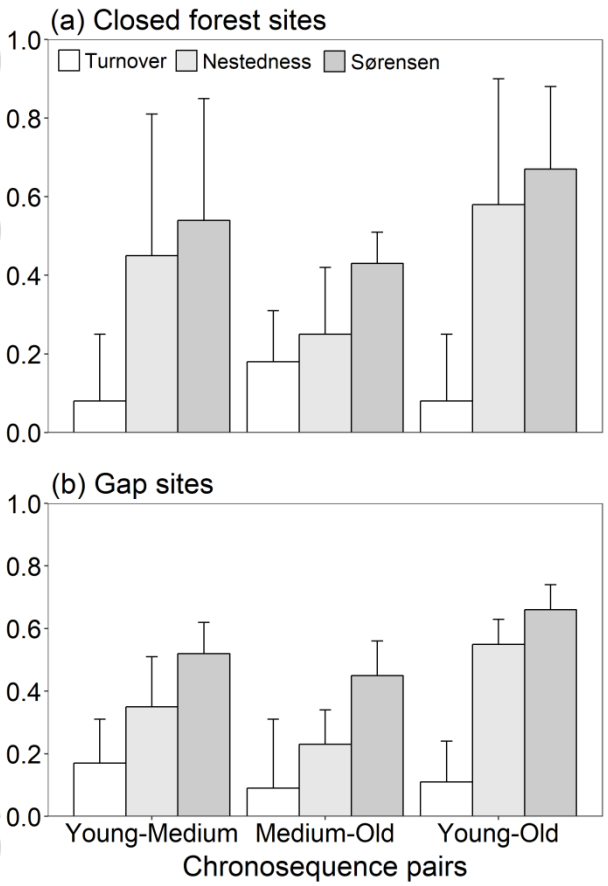

Figure 3. Average "temporal" turnover (white) and nestedness (grey) components of Sørensen dissimilarity (dark grey) between epiphyll communities on groups of differently-aged leaves within closed-forest (a) and gap sites (b) in the rain forest of Barro Colorado Island (Panama). Shown are means of all sites with standard deviations. No differences (p>0.05) were found between closed-forest and gap sites (Mann-Whitney test).

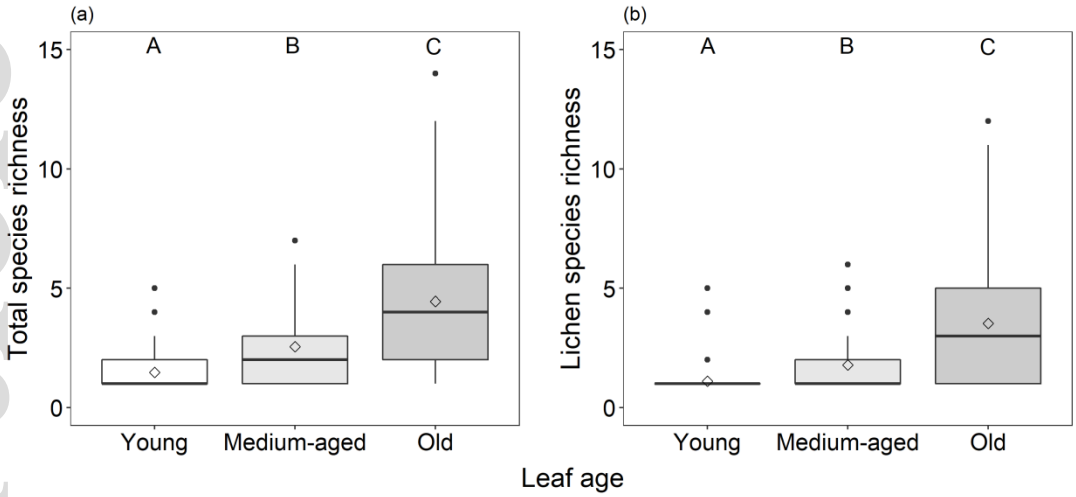

Figure 4. Total epiphyll (a) and epiphyllous lichen (b) richness as a function of leaf age for leaves collected in gaps and closed forest on Barro Colorado Island (Panama). Box plots represent the quantiles, open diamonds represent the means. Significantly different groups according to Tukey-adjusted comparisons are marked by different letters (Table 1, Appendix S14).

Appendix S1. Studied site characteristics.

Appendix S2. Occurrence of species and morphospecies on leaves.

Appendix S3. Microclimate in closed forest and gaps.

Appendix S4. Turnover and nestedness components of Sørensen dissimilarity between epiphyll communities on leaves within closed forest and gaps and among these microsites.

Appendix S5. Turnover and nestedness, components of Sørensen dissimilarity within closed forest and gaps for different leaf age groups.

Appendix S6. Canonical correspondence analysis of epiphyllous lichen and liverwort communities in relation to environmental gradients.

Appendix S7. Total lichen and liverwort occurrence probability on leaves.

Appendix S8. Algal cover and occurrence probability in relation to environmental factors.

Appendix S9. Fungi cover and occurrence probability in relation to environmental factors.

Appendix S10. Total epiphyll, epiphyllous lichen and liverwort cover on leaves in two microsites according to environmental factors.

Appendix S11. Total epiphyll species richness and cover in relation to environmental factors.

Appendix S12. Epiphyllous lichen species richness and cover in relation to environmental factors.

Appendix S13. Epiphyllous liverwort species richness and cover in relation to environmental factors.

Appendix S14. Tukey-adjusted comparisons of interactions for epiphyllous species occurrence probability, richness and cover on leaves.